Distance decay of similarity in fungivorous insect communities: Assessing dispersal limitation using genetic data

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Distance decay of similarity in fungivorous insect communities: assessing dispersal limitation using genetic data

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Abstract. We evaluated how dispersal limitation affected spatial variation in the species composition of fungivorous insect communities inhabiting fruiting bodies of bracket fungi on scattered deadwoods. The insect communities showed significant distance decay of similarity pattern among deadwoods, which was not fully explained by differences in environmental conditions. To investigate whether insect dispersal limitation could explain the distance-decay pattern, we analyzed mitochondrial haplotype data; limited dispersal is expected to generate an isolation-by-distance pattern of genetic structure in component species. However, genetic distance between deadwoods was not correlated with geographic distance in any species, and a simulation study suggested that the absence of genetic structure refutes the dispersal limitation hypothesis even when the resolution of genetic differences is not high, as in our study. Thus, dispersal limitation did not contribute to the observed community patterns within our study site, suggesting that unmeasured environmental factors may have played an important role. Our study demonstrates that genetic data can help determine whether dispersal limitation of component species is the primary cause of observed distance decay in community similarity.

Key words: community similarity; dispersal limitation; distance decay; fungivorous insect; genetic structure; habitat filtering; metacommunity; spatial analyses.

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Introduction

Distance decay of similarity in ecological communities is a typical spatial pattern in biodiversity, and refers to cases where the similarity in species composition between communities decreases as the geographic distance between them increases (Nekola and White 1999). Analyzing the negative relationship between distance and similarity provides insight into the mechanisms that influence community structure and biodiversity.

The causes of distance decay can be categorized into two general types: niche-based processes and dispersal-based processes (Condit et al. 2002, Cottenie 2005). The niche-based processes include a combination of habitat filtering and competitive exclusion (Cornwell et al. 2006). In niche-based processes, local environmental conditions and species' characteristics constrain species' colonization abilities, survival, reproductive rates, and competitive dynamics. If these environmental variables are spatially structured, we should expect corresponding spatial patterns in species composition. In contrast, dispersal-based processes can generate spatial patterns in species composition through organisms' dispersal behavior. For example, if some species have an extremely limited ability to disperse and the individuals of each species show aggregated distribution regardless of environmental

heterogeneity, the community can be perceived to be spatially structured. Dispersal-based processes are often referred to as neutral processes because, in neutral community models, they can generate spatial structure without any ecological differences among individuals (Bell 2001, Hubbell 2001).

It is challenging to distinguish between the effects of these two processes on community similarity using only datasets of species abundance (or presence/absence) and environmental variables. In recent studies on the relative importance of niche- and dispersal-based processes in community assembly, spatial signatures in community structure that appear to be unrelated to environmental factors have frequently been attributed to underlying dispersal processes (Tuomisto et al. 2003, Cottenie 2005, De Bie et al. 2012, Winter et al. 2013). However, this interpretation depends heavily on the completeness and quality of environmental data (Jones et al. 2008); unmeasured spatially structured environmental variables may also affect species composition. Chang et al. (2013) demonstrated that including essential environmental predictors can increase the perceived importance of niche-based process. Their study implied that there is a tendency to overestimate the role of dispersal-based processes in shaping the spatial structure of communities. Therefore, more complete and accurate information about patterns of dispersal is required to achieve more reliable insight into the spatial patterns of communities.

Molecular genetics has been used in population ecology to examine the relationship between dispersal and spatial synchrony in population dynamics (Liebhold et al. 2004) and spatial autocorrelation in abundance (Stacy et al. 1997, Schwartz et al. 2002, Koizumi et al. 2008). When synchrony is caused by frequent migration between two populations, the genetic differentiation between them is expected to be low. Molecular genetics can therefore be applied to investigate the influence of dispersal on the spatial structure of communities; if spatial genetic differentiation is low for component species, this implies high dispersal rates among local habitats and low potential for development of spatial variation in community structure. Recent macroecological studies have focused on community-level distance-decay patterns by linking them with the spatial genetic structure of component species (Papadopoulou et al. 2011, Baselga et al. 2013). This approach leads to better understanding of the role of dispersal limitation.

The importance of environmental heterogeneity and dispersal processes is assessed in the metacommunity framework (Leibold et al. 2004). "Metacommunity" describes a set of local communities that are linked by the dispersal of multiple potentially interacting species (Wilson 1992). Models of metacommunity dynamics are based on discrete local communities or habitat patches. Therefore, discrete habitats that have naturally defined spatial boundaries are ideal systems for investigating the importance of dispersal in structuring communities within a metacommunity framework. Sporocarps (fruiting bodies) of wood-decaying bracket fungi are habitats for fungivorous insects, and provide excellent model systems for studying population and community dynamics in patchy environments (Hanski 1989). Brackets of wood-decaying fungi form discrete habitats and are clearly discontinuous at two levels: at the level of sporocarps and at the level of the deadwoods on which they grow. Here, we define an ecological community as a group of individuals and species within the same trophic level that potentially compete in a local area for the same resources. Our analysis includes only fungivorous species inhabiting sporocarps that potentially compete with each other. Dispersal among sporocarps is typically carried out by ovipositing females.

In this study, we used fungivorous insect communities to evaluate the influence of dispersal processes on species-assemblage structure. Using mitochondrial haplotypes, which are maternally inherited genetic markers, we examined the genetic structure of three dominant species comprising this spatially structured community at the two levels of sporocarps and deadwoods. If dispersal limitation among habitats exists, we should expect the genetic structure of insects to follow patterns related to the geographic distances between habitats. On the other hand, when genetic dissimilarity does not increase with physical distance, spatial structure at the community level is likely to be caused by other factors (e.g., spatially autocorrelated environmental conditions and environmental niche differences

among species). Moreover, we performed simulations to examine whether the resolution of our genetic analysis was sufficient to detect isolation-by-distance pattern caused by limited dispersal.

Materials and Methods

Surveys of fungivorous insect communities

We studied fungivorous insect communities in sporocarps of the bracket fungus *Trametes orientalis* within a 1-km^2 area of secondary broad leaf forest at Mt. Uryu in Kyoto, western Japan (35°2′00″–2′33″ N, 135°47′50″–48′30″ E; elevation 100–300 m a.s.l.; Appendix S1: Fig. S1). The sporocarps of *T. orientalis* grow predominantly on snags and downed logs of dead oaks; in the study area, these were mostly *Quercus serrata* and *Quercus variabilis*. The sporocarps are typically annual, although sometimes dead sporocarps remain attached to wood and produce new hymenia the following year. Between June 1 and 5, 2013, we sampled up to four *T. orientalis* sporocarps per deadwood and a total 405 sporocarps of *T. orientalis* from 113 deadwoods. Geographic coordinates (latitudes and longitudes) for each sampled deadwood were recorded using a handheld Garmin 62s GPS device (Garmin International, Olathe, Kansas, USA). The sporocarps were brought to a laboratory, weighed, and preserved in 99% ethanol within 24 h of sampling. Insects were collected from preserved sporocarps under a stereoscopic dissecting microscope and preserved in 99% ethanol. After insects were removed, sporocarps were dried on a hotplate at 45°C for more than 24 h and weighed to determine their dry weights and water contents. The weight of insects was assumed to be negligible.

Environmental variables

We used six variables to characterize local environmental conditions: elevation, convexity, aspect, number of sporocarps, and average dry weight and water content of sporocarps on each deadwood. Elevations were obtained from GPS data. We calculated convexity and aspect following De Caceres et al. (2012). First, we divided the study area into 50 × 50-m quadrants and calculated the mean elevation of the four corners of each quadrant. Next, we calculated convexity from the elevation of focal quadrant minus the mean elevation of the eight surrounding quadrants. We initially calculated aspect as degrees from north using the formula in De Caceres et al. (2012), and then segmented it into two values for east–west and north–south directions.

Genetic analysis for dominant species

Genetic analyses focused on three species that are dominant in *T. orientalis* sporocarps: the pleasing fungus beetle (*Aulacochilus sibiricus*), ciid beetle (*Octotemnus laminifrons*), and fungus gnat (*Asioditomyia japonica*). Because the sample sizes of these three species were very large, we randomly selected communities on 40 deadwoods and analyzed 3612 individuals from 149 sporocarps. To determine whether larvae on each deadwood tended to be derived from eggs deposited concurrently and by the same female, we assigned *A. sibiricus* and *A. japonica* larvae in each sporocarp to age classes according to their head width (see Appendix S2: Fig. S1).

Total genomic DNA was extracted using a Genomic DNA Purification Kit (Promega, Madison, Wisconsin, USA) for *O. laminifrons* and *A. japonica*. For *A. sibiricus*, DNA extraction was performed following a method introduced by the Transgenic Mouse Facility, University of California Irvine (available online at http://www.research.uci.edu/facilities-services/tmf/technical-advice/dna-prep.html), with slight modifications.

We used haplotype-specific PCR (polymerase chain reaction) to determine the mitochondrial haplotype of each individual. First, to catalog mitochondrial haplotypes for each species, we randomly selected 96 individuals per species, PCR-amplified 668–695 base pair (bp) fragments of the cytochrome oxidase I (COI)–cytochrome oxidase II (COII) region using species-specific primers (Appendix S3: Table S1), and sequenced the PCR products using an ABI 3130xl sequencer (Applied Bio-Systems, Foster City, California, USA). For *O. laminifrons*, we also sequenced an 830-bp region of NADH (nicotinamide adenine dinucleotide hydride) dehydrogenase subunit 5 (ND5) because the COI–COII region revealed few haplotypes. Next, we designed haplotype-specific PCR primers to distinguish among haplotypes (Appendix S3: Table S1). A primer set for a species included a forward (F)

and reverse (R) common primer and multiple forward haplotype-specific primers, with the 3′ terminal base of each specific primer matching one of the SNPs characterizing the haplotype. A mismatch was introduced to the third base from the 3′ end of each haplotype-specific primer to increase haplotype specificity. PCR products were electrophoresed on 2.0% agarose gels to determine haplotype based on the presence/absence patterns of each PCR product.

Statistical analyses

We analyzed species composition, including all five species collected from sporocarps. However, genetic analyses used only three of the five species.

Analysis of similarities.—To test whether species, haplotype, or age compositions in sporocarps were more similar to one another among sporocarps within a given deadwood than among deadwoods, we used analysis of similarities (ANOSIM) (Clarke 1993), which is a nonparametric test for comparisons between groups. The ANOSIM test statistic R was calculated as the differences within vs. between deadwoods in the averaged ranks of pairwise dissimilarity. $R = 0$ indicates no effect, and R close to unity indicates a strong effect of deadwood identity on community composition. We used the Morisita–Horn index (eq. 14 in Wolda [1981]) as a measure of dissimilarity in species composition and age structure. This quantitative dissimilarity index is independent of sample size and species richness (Wolda 1981) and is hence appropriate for our fungivorous insect community, where community size and species richness were variable and partly dependent on habitat size. All zero values in community matrices were replaced by small positive values (0.01) before the calculation. As a measure of genetic distance, Nei's average number of differences between populations D_A (Nei and Li 1979) was calculated using the program ARLEQUIN version 3.0 (Excoffier et al. 2005). We used populations larger than five in the calculation of D_A. The ANOSIM statistic R and Morisita–Horn index were calculated using the package "vegan" (Oksanen et al. 2013) in the statistical language R version 2.15.3 (R Development Core Team 2013). The significance of R was determined using 10,000 permutations.

Quantification of spatial structure.—To quantify the spatial structure of species and haplotype compositions among deadwoods, we first conducted Mantel tests. For the Mantel tests, we computed the dissimilarity matrices of species composition (Morisita–Horn index) and genetic distance (D_A) between all pairs of deadwoods. Their correlations with geographic distance matrices (Mantel's r) were calculated, and the significance was determined based on 20,000 permutations. Although Mantel tests are widely used in spatial analysis, they have been criticized for having less power to detect spatial autocorrelation in the response data (Legendre et al. 2015). Redundancy analysis (RDA), which uses distance-based Moran's Eigenvector Maps (dbMEMs, formerly called PCNMs [Borcard and Legendre 2002, Dray et al. 2006]) is suggested as an alternative method with higher power for detecting spatial structure in data compared with Mantel tests (Legendre et al. 2015). Therefore, we also conducted RDA with dbMEMs to confirm the robustness of the statistical inferences from the data. In both analyses, all individuals of a species or haplotypes sampled from sporocarps on a given deadwood were pooled into a single population. For RDA, We constructed dbMEMs, which provide variables that quantify spatial structure. We performed the following steps to obtain the dbMEM variables (Borcard et al. 2011): (1) construct the Euclidean distance matrix among all sites; (2) determine a truncation threshold, *thresh*, that is, the maximum value of the minimum spanning tree of Euclidean distance matrix; (3) modify the distance matrix by changing all distances larger than the truncation distance to ($4 \times$ *thresh*); (4) compute the principal coordinates of that matrix; (5) use the eigenfunctions that model positive spatial correlation (i.e., Moran's I larger than expected value of I) of the dbMEMs as spatial descriptors in RDA. The species and haplotype data matrices were Hellinger transformed to avoid considering the absence of the individuals as a resemblance between observations (Legendre and Gallagher 2001). We calculated unbiased estimates of variation explained by dbMEMs based on RDA using an adjusted R^2 (hereafter R^2_a; Peres-Neto et al. 2006). The significance of the explained fraction was tested using 999 permutations.

Variation partitioning.—To decompose the variation in species composition into fractions explained by pure environmental factors (the spatial component of environment removed), pure spatial predictors (the environmental component of space removed), and the covariance between environmental factors and spatial predictor (*Shared*), we used the variation partitioning approach (Borcard et al. 1992). We used eigenfunctions of dbMEM as spatial variables and the six environmental variables described above to represent the environment. We used the forward selection method (Blanchet et al. 2008) to extract significant dbMEMs and environmental variables before conducting variation partitioning. The construction of dbMEM variables, calculation of R^2_a, and test of their significance were conducted as described above.

Simulation study on the effect of haplotype number on the resolution of genetic structure analysis

Low resolution of genetic structure due to a limited number of haplotypes per species might preclude detection of isolation-by-distance patterns caused by limited dispersal. To address this possibility, we examined the relationship between community and genetic structure with various combinations of dispersal distance and haplotype number using a custom program written in R (Supplement S1). We examined whether we could detect significant spatial genetic structures (correlation between genetic and geographic distance) in component species with a given number of haplotypes (particularly 4–6, the number used in our study) when distance decay of similarity in species composition has been generated through limited dispersal.

We defined a lattice of 30 × 30 sites in which the distance between the closest sites was one unit. Our simulation started with six species, each with 12 haplotypes, distributed randomly across the sites. Average initial population size at each site was 72. The process of dispersal and reproduction was as follows: (1) each individual undertakes dispersal in a random direction with a distance r, which is determined according to the probability $k(r) = (1/m) \exp(-r/m)$, where m is the mean dispersal distance; (2) each dispersed individual deposits 100 offspring at the nearest site; (3) at each site, 99% of all offspring die randomly. Steps (1) to (3) were repeated for 500 generations, for 25 combinations of five mean dispersal distance (m = 0.25, 0.5, 1, 2, 4) and five haplotype numbers (N_h = 2, 3, 4, 6, 12), which included the actual number of haplotypes per species used in this study. For each mean dispersal distance, we conducted 100 replicate simulations. To reduce edge effects, subsequent analyses of the simulation results used only data from the central 20 × 20 sites. As our field study was conducted within an area of 1000 × 1000 m, the unit distance in the simulation corresponds to roughly 50 m.

We then computed dissimilarity of species composition using the Morisita–Horn index and the genetic distance measure D_A between all pairs of sites at the species and haplotype levels, respectively, and assessed the significance of its correlation with distance by Mantel test. We also conducted dbMEM analysis based on RDA. The dbMEM analysis procedure was the same as that for empirical data. We calculated the proportion of cases where no significant correlation between distance and D_A or no significant R^2_a was observed in any species despite there being significant distance decay or R^2_a species composition similarity for different dispersal distances and different haplotype resolutions.

Results

Spatial structure of similarity in species compositions

In total, 11,015 individuals were sampled, and more than 99.5% of insect fungivores were identified at the species level (Appendix S2: Table S1). The species composition in a sporocarp was significantly more dissimilar among than within deadwoods (Fig. 1a, Table 1). At the deadwood level, where all individuals in sporocarps within a deadwood were pooled into one community, similarity in species compositions showed significant spatial structure with both the Mantel test and RDA; community dissimilarity was significantly correlated with geographic distance (Fig. 2a, Table 1), and the dbMEM variables explained 29.2% of the variation (Table 1). These results demonstrated a distance-decay pattern of community similarity.

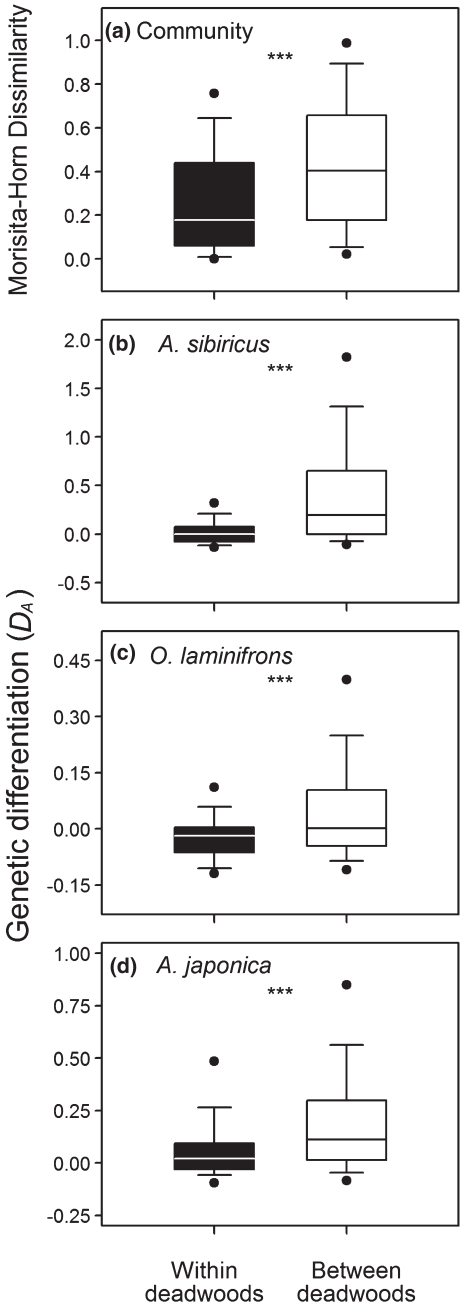

Fig. 1. Box plot of (a) species compositional dissimilarity and (b–d) pairwise genetic distance D_A values for three component species within deadwoods (solid boxes) and between deadwoods (open boxes). The middle horizontal line represents the median, and the vertical edges of each box represent the 25th and the 75th percentiles of distribution; whiskers extend to the 10th and the 90th percentiles. The 5th and 95th percentiles are shown as points. ***$P < 0.001$, for ANOSIM, by 20,000 permutations.

Species composition and environmental variables

The forward selection procedure retained nine dbMEM eigenfunctions for modeling species composition with spatial variables, and only elevation among environmental variables. The effect of elevation was highly spatialized (97.2% of the variation; Fig. 3). However, elevation explained only 19.8% of the spatially structured variation in species composition (Fig. 3). It is therefore possible that the patterns of community dissimilarity at the deadwood level were due to limited dispersal of the component species.

Spatial patterns in genetic differentiation and age structures

We discriminated six haplotypes each for *A. sibiricus* and *A. japonica* and four haplotypes for *O. laminifrons* (sequence data are deposited at the DNA Data Bank of Japan [DDBJ]; accession nos. LC093871–LC093887). In all three species, genetic distances among sporocarps within deadwoods were significantly smaller than those between deadwoods (Fig. 1b–d, Table 1). Larval age structures (Appendix S2) were significantly more similar among sporocarps within than among deadwoods for both *A. sibiricus* ($R = 0.496$, $P < 0.001$) and *A. japonica* ($R = 0.237$, $P = 0.002$), suggesting that larvae within a deadwood were often siblings. Despite the significant distance decay of community similarity with geographic distance, the correlation between genetic and geographic distances was not significant in any of the three species in Mantel tests (Fig. 2b–d, Table 1), and the variation of genetic structure explained by dbMEM variables was also not significant in any of three species in RDA (Table 1).

Simulation results

As expected, both Mantel's r and R^2_a of RDA for species composition and haplotype composition for each species became less evident with increasing dispersal distance. At a given dispersal distance, Mantel's r or R^2_a for haplotype composition also became smaller with decreasing haplotype number (Fig. 4a–d). However, the proportion of cases in which no significant Mantel's r or R^2_a was observed in any species despite significant distance decay of community similarity was less than 5%, hence negligible,

Table 1. Results of ANOSIM, Mantel, and RDA analyses quantifying the spatial structures in species and haplotype compositions.

Analysis	Community level	Within species level		
		A. sibiricus	*O. laminifrons*	*A. japonica*
Within-deadwood				
ANOSIM's R	0.473	0.512	0.264	0.353
P value	<0.001	<0.001	<0.001	<0.001
Among-deadwood				
Mantel's r	0.159	0.034	0.034	0.029
P value	<0.001	0.355	0.356	0.371
Adjusted R^2	0.292	0.145	0.145	−0.119
P value	<0.001	0.089	0.101	0.959

when four to six haplotypes were available, as in our empirical study, and the mean dispersal distance was as short as 0.25—1.00, which may correspond to 12.5—50 m at our field site (Fig. 4e, f). Note that RDA had higher power than Mantel's r for detecting spatial structure in species composition resulting from weak dispersal limitation (i.e., when dispersal distance was ≥1; Fig. 4e, f).

Discussion

Our field data on a fungivorous insect community showed that genetic distance was not correlated with geographic distance for component species (Fig. 2b–d). This result is inconsistent with the distance decay pattern in species compositional similarity of the insect community (Fig. 2a). Low levels of genetic differentiation might reflect the absence of dispersal limitation (Slatkin 1985), and estimates of genetic differentiation are sometimes correlated with independent estimates of demographic observations from the same populations (Miller et al. 2002, Vandewoestijne and Baguette 2004). In this study, the lack of correlation between genetic and geographic distances implies that dispersal rates between deadwoods did not decay substantially with distance. Although it is possible that our ability to detect genetic structure was limited by the low numbers of haplotypes in our study, our simulation study confirmed that 4–6 distinct haplotypes were enough to detect the genetic isolation-by-distance pattern. Therefore, the discordance between genetic and community dissimilarity patterns implies that the effects of dispersal limitation on spatial community structure were negligible. This result contrasts with that of previous large-scale studies of beetle communities in the Aegean Islands (Papadopoulou et al. 2011) and Europe (Baselga et al. 2013), which revealed a concordant pattern of species and genetic diversity.

Leibold et al. (2004) categorized metacommunity paradigms into four types: species sorting (SS), mass effect (ME), patch dynamics (PD), and neutral (NW). These paradigms differentially emphasize the role of dispersal, heterogeneity in local habitat conditions, and species ecological similarity. While the ME, PD, and NM paradigms require dispersal to be limited, a necessary underlying assumption for SS to structure communities is that dispersal is sufficiently high for species to colonize the sites with suitable environmental conditions. Given that dispersal limitation was not detected in this study, the system studied here may be subject to SS, although specific environmental predictors that actually structure communities were not identified. Given that the observed distance decay pattern was not generated through dispersal processes, unmeasured environmental variables that are spatially autocorrelated may explain the remaining variation in species composition (Chang et al. 2013). For fungivorous insects, fungal taxa have been examined as a major factor affecting species composition (Komonen 2001, Yamashita and Hijii 2003). However, because we examined only one fungal species in this study, our results suggest that other environmental conditions also contribute to the species assemblage of fungivorous insects. Although we initially expected topological

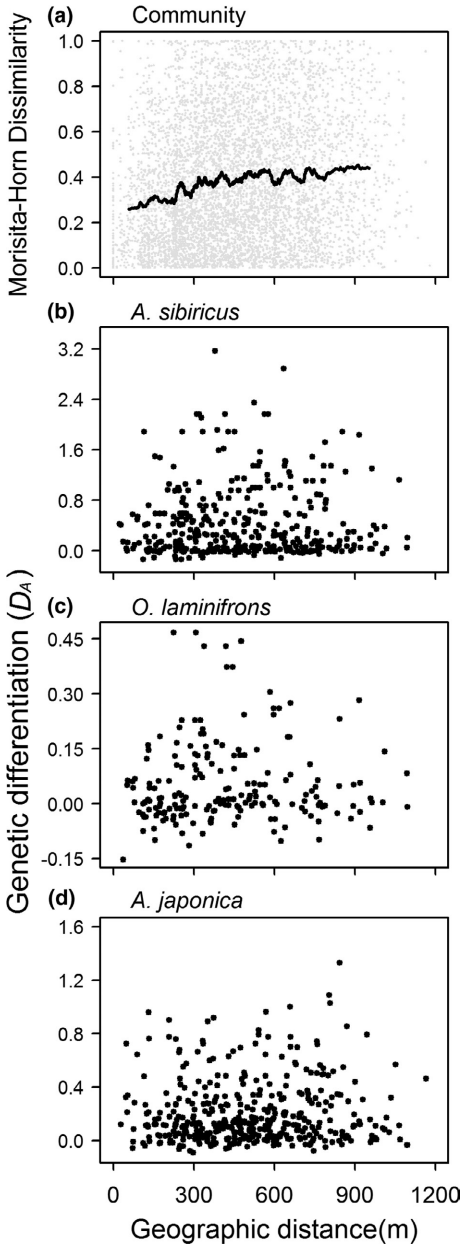

Fig. 2. Relationships between geographic distance and (a) community dissimilarity and (b–d) genetic distance D_A for three component species. Solid line denotes the moving average determined over a window including 300 points.

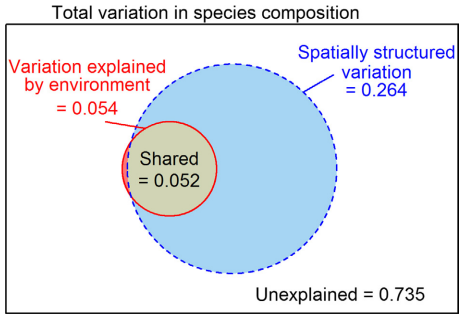

Fig. 3. Venn diagram of variation partitioning of the response dataset (species composition) using two sets of explanatory variables: environmental variables (left circle: environment) and dbMEM eigenfunctions (right circle: space). The rectangle represents the total variation in the species composition. The reported fractions are R^2_a statistics.

variables (as proxies of microclimate conditions) to be major factor that explained spatially structured variation in species composition, only altitude among the measured variables explained less than 20% of the spatially structured variation. The spatial aggregation of predator and parasitoids (Driessen and Hemerik 1991) and intraspecific variation in sporocarp quality are potential factors because we focused on one trophic level (fungivores).

In contrast to the pattern at the between-deadwood level, genetic differentiation and species compositional dissimilarity were concordant at the within-deadwood level. Compositional similarity among sporocarps within a deadwood can result from certain female oviposition patterns; for example, when one female oviposits simultaneously at multiple sporocarps on the same deadwood. The existence of such a pattern was supported by our observation that age structures of *A. sibiricus* and *A. japonica* larvae were more similar within than between deadwoods. Therefore, the similarity in species composition among sporocarps on a deadwood could be explained by some combination of female ovipositing pattern (i.e., the dispersal process) and similarity in environmental conditions.

Unlike *A. sibiricus* and *A. japonica*, we sampled *O. laminifrons* mainly at the adult stage. This species is univoltine and emerges as adults in summer; most individuals remain in their existing sporocarp habitats during the winter and disperse to new sporocarps in spring (Kawanabe 1998). In this study, we carried out sampling after the spring dispersal. Therefore, the lower levels of genetic differentiation within deadwoods (compared to between deadwoods)

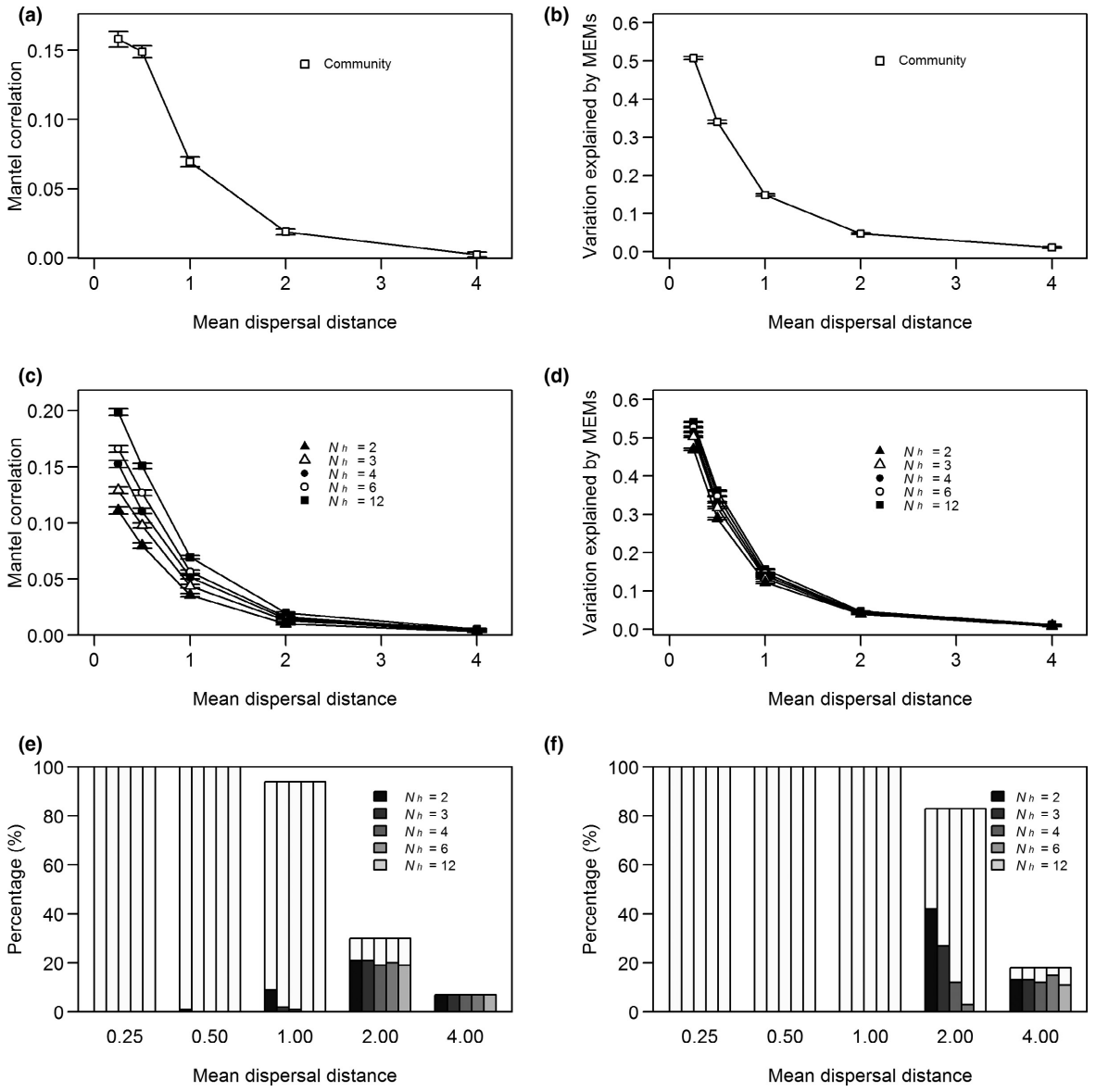

Fig. 4. Mantel correlations and R^2_a for (a, b) community and for (c, d) haplotypes for varying number of haplotypes (N_h) in component species, against mean dispersal distance. Error bars represent standard errors. (e, f) Percentage of cases where a significant Mantel correlations and R^2_a for community was observed (white bars), and where no significant Mantel correlations and R^2_a for haplotypes was observed in any species (gray bars).

might be due to adult individuals dispersing at higher rates within deadwoods than between deadwoods.

In this study, the addition of genotype data allowed us to determine whether dispersal limitation could lead to distance decay of community structure. Our approach is applicable to a wide range of communities and will help refine our understanding of how dispersal and other factors shape the spatial structure of communities.

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